



Disturbance Regimes and Mountain Plover Habitat in Shortgrass Steppe: Large Herbivore Grazing Does Not Substitute for Prairie Dog Grazing or Fire

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ABSTRACT Restoring historical disturbance regimes to enhance habitat for grassland birds can conflict with livestock production goals and has been controversial because of uncertainty in the frequency and pattern of different disturbances prior to European settlement. We studied nesting habitat for the mountain plover (*Charadrius montanus*) in relation to prescribed fire, grazing by large herbivores (cattle), and grazing by black-tailed prairie dogs (*Cynomys ludovicianus*) in the shortgrass steppe of northeastern Colorado. Breeding mountain plovers primarily occurred on black-tailed prairie dog colonies or areas burned during the previous dormant season. Vegetation surrounding mountain plover nests and foraging locations was characterized by a fine-scale mosaic of prostrate (<4 cm tall) vegetated patches interspersed with >35% bare soil in a given square meter, with this fine-scale pattern distributed over a broad (>100-m radius) area. Mountain plovers rarely occupied grassland lacking prairie dogs or recent fire, but those that did selected sites with similar vegetation height and bare soil exposure as sites on burns and prairie dog colonies. Vegetation structure at mountain plover-occupied sites was also similar to random sites on burns and prairie dog colonies, but differed substantially from sites managed only with cattle. Intensive cattle grazing at twice the recommended stocking rate during spring (Mar–May) or summer (May–Oct) for 6 years produced significantly less bare soil than burns and prairie dog colonies, particularly following years with average or above-average precipitation. Thus, intensive cattle grazing did not substitute for prairie dog grazing or fire in terms of effects on vegetation structure and mountain plover habitat. Both prescribed burning and increased size and distribution of black-tailed prairie dog colonies appear to be effective and complementary means to manage for mountain plover breeding habitat in shortgrass steppe. Provision of mountain plover habitat has tradeoffs with traditional management for livestock production. Thus, managers need to clearly define desired outcomes for management to provide multiple ecosystem goods and services. © 2012 The Wildlife Society.

KEY WORDS black-tailed prairie dogs, *Cynomys ludovicianus*, ecosystem management, grassland birds, historical range of variation, livestock grazing, prescribed fire, rangeland management, spatial heterogeneity, vegetation structure.

Fire and grazing are disturbances that historically influenced the structure, function, and biodiversity of grassland ecosystems (Frank et al. 1998, Fuhlendorf and Engle 2004, Samson et al. 2004). However, historical spatial and temporal patterns of grazing and fire are often difficult to assess in grassland ecosystems. For example, fire was not identified as a historical disturbance in the shortgrass steppe of central North America (Peters et al. 2008), whereas fires reportedly occurred at <12-year return intervals in grasslands both east (greater precipitation) and west (less precipitation) of the shortgrass steppe (McPherson 1995, Brown and Sieg 1999). Similarly, efforts to estimate the spatial scale and intensity of grazing by bison (*Bison bison*) prior to European settlement

are characterized by substantial untestable assumptions and high uncertainty (Bamforth 1987, Hart 2001). Moreover, the restoration of disturbance regimes for contemporary wildlife conservation objectives can be at odds with traditional management for livestock production (Fuhlendorf and Engle 2001, Samson et al. 2004). As a result, assessments of ecosystem management for grasslands often focus on the amount and distribution of land that has been converted to cropland or other uses, rather than on disturbance regimes operating within remaining native grassland (Samson et al. 2004).

Ecosystem management based on historical disturbance regimes can be informed by considering the habitat requirements of individual species (Hauffer et al. 1996, Hutto 2008). Recently, concerns have been raised about how changes in disturbance regimes in the Great Plains of central North America may be linked to large-scale declines of some

Received: 20 May 2011; Accepted: 19 August 2011;
Published: 6 January 2012

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breeding birds (Brennan and Kuvleskey 2005). Variation in vegetation structure in grasslands, which is influenced by grazing and fire, is a key determinant of breeding bird communities (Knopf 1996, Fuhlendorf et al. 2006, Derner et al. 2009). However, studies evaluating how the management of different disturbances is linked to bird conservation in semiarid grasslands have been lacking.

The mountain plover (*Charadrius montanus*) is a native grassland bird of the western Great Plains whose populations declined substantially between the 1960s and 1990s (Knopf and Wunder 2006). It has been identified as a species of conservation concern by the United States Fish and Wildlife Service, the United States Forest Service, and the states of Colorado, Kansas, Nebraska, Wyoming, and Montana. Most of the historical breeding range for this migratory species occurred in the western Great Plains, with additional populations in shrub steppe and montane rangelands immediately west of the Great Plains (Knopf and Wunder 2006). Common features of mountain plover nesting habitat are prostrate vegetation and greater percentages of bare soil (Olson and Edge 1985, Knopf and Miller 1994, Plumb et al. 2005). Such habitat conditions arise from the combined influence of semiarid to arid climates, where moisture availability limits plant cover, and disturbance by grazers and fire. In the shortgrass steppe of the southwestern Great Plains (Lauenroth et al. 1999) breeding mountain plovers occur in grasslands grazed by livestock and lacking prairie dogs (Knopf and Miller 1994), but substantially greater densities occur on black-tailed prairie dog colonies and recent burns (Tipton et al. 2009, Augustine 2011). Because prairie dogs can compete with livestock (Derner et al. 2006), some livestock producers and range managers have questioned whether intense livestock grazing, in the absence of prairie dogs, could generate mountain plover habitat. Restoration of the historical role of fire has also been suggested as a potential means to create habitat for mountain plovers and other declining wildlife (Thompson et al. 2008, Knopf 2008, Augustine 2011), but has been controversial because of perceived loss of forage for livestock. This again raises the question of whether intense livestock grazing could achieve the same result.

We examined mountain plover nesting habitat in shortgrass steppe in relation to prescribed fire, grazing by black-tailed prairie dogs, and grazing by cattle. Our study area was formerly considered a breeding stronghold for mountain plovers (Graul and Webster 1976), but declining populations over the past 4 decades call into question whether moderately grazed grassland, as studied by Graul (1975) and Knopf and Miller (1994), can support viable plover populations. Previous measurements at mountain plover nests in moderately-grazed grassland in 1992 found approximately 30% bare soil within a square meter surrounding nests, but significantly less bare soil 25–50 m from nests (Knopf and Miller 1994), raising the question of whether the spatial pattern of vegetation surrounding nest sites may influence habitat suitability. During the 1990s, mountain plover densities declined substantially in the area (Knopf 2008). However, over the past 15 years, the area occupied

by black-tailed prairie dog colonies has increased by an order of magnitude, a prescribed burning program was initiated, and substantially greater mountain plover densities have been observed on prairie dog colonies and prescribed burns compared to moderately-grazed grassland (Augustine 2011).

Our first objective was to quantify vegetation structure at sites where mountain plovers nest and forage, and compare with sites located on black-tailed prairie dog colonies, prescribed burns, and moderately-grazed grassland. We sought to quantify temporal and spatial heterogeneity in vegetation structure at sites used by mountain plovers, in order to examine 1) the magnitude of interannual variation in habitat structure, and 2) test whether mountain plovers chose nest sites based on spatial vegetation patterns, rather than just mean values of vegetation cover. Additionally, we sought to assess vegetation conditions resulting from intense grazing by cattle. We specifically evaluated cattle grazing at double the recommended stocking rate in spring (Mar–May) or summer (May–Oct) and compared resulting vegetation to that on prescribed burns and prairie dog colonies, as well as that measured at mountain plover nesting and foraging sites.

STUDY AREA

We studied approximately 60,900 ha of publicly managed grassland on Pawnee National Grassland and Central Plains Experimental Range in northeastern Colorado (Augustine 2011). The climate was semiarid, with cold, dry winters; most precipitation fell as rain between April and September (Lauenroth and Milchunas 1992). Long-term mean annual precipitation was 355 mm with annual precipitation from 2006 to 2009 being 250 mm, 331 mm, 317 mm, and 379 mm, respectively. Topography was flat to gently undulating, with slopes typically 0–3%. Soils were predominantly fine sandy loams and loams. Vegetation was dominated by perennial, grazing-tolerant shortgrasses (Lauenroth and Milchunas 1992).

METHODS

Vegetation Structure at Mountain Plover Nesting and Foraging Sites

Each of 4 years (2007–2010), we 1) conducted an initial survey between 21 April and 7 May at a large number of sites including burns, prairie dog colonies, and grassland with no recent history of fire or prairie dog disturbance to identify sites with breeding plovers, 2) conducted a second survey between 27 April and 13 May at those sites where we previously detected plovers, in order to locate nests or foraging locations of mountain plovers, and 3) measured vegetation structure surrounding nesting and foraging locations. We completed vegetation structure measurements by 13 May each year to minimize the effect of plant phenology.

For the initial survey in 2007, we systematically drove the area in a 4-wheel drive vehicle and stopped at 100–200 m intervals to scan for mountain plovers with 8 × 42 binoculars (Dinsmore et al. 2005). Vehicles are recommended for use in mountain plover surveys because flushing distances may be

within 3 m for vehicles, but 50–100 m for humans approaching on foot (U.S. Fish and Wildlife Service 2002). For the initial surveys in 2008–2010, we conducted point counts in a systematic grid at each site, with 250-m spacing between points (Augustine 2011). The observer drove to each point using an all-terrain or 4-wheel drive vehicle, and then exited the vehicle for the point count. The initial surveys included varying numbers of burns and prairie dog colonies each year (Appendix 1) plus 3 grassland sites with historical records of breeding mountain plovers (non-random grassland sites in Appendix 1). We also surveyed 12 randomly selected grassland sites in 2008 and 2009. Because we did not detect plovers at randomly selected grassland sites in 2008 or 2009 (Augustine 2011), we reallocated this survey effort to prairie dog colonies in 2010 by searching both large (>16 ha) and small (<16 ha) colonies in the study area. Prior to 2010, we only surveyed prairie dog colonies larger than 16 ha.

For the second survey (conducted each year at sites where plovers were detected in the initial survey) we systematically drove the area in a 4-wheel drive vehicle, again stopping at 100–200 m intervals to scan for mountain plovers. We observed each plover detected until we found its nest or observed behaviors indicating the bird did not have a nest. For each detection, we noted the first location where the bird foraged. We either recorded the geographic coordinates of the nest (nest locations), or if no nest was found, the coordinates of the first location where the bird foraged (foraging locations). We recorded nest or foraging locations for >1 plover at a site only if we could verify they were different birds, and we only recorded either a nest or a foraging location for each bird.

For each foraging and nest location, we measured vegetation height, foliar cover, and litter cover in a systematic grid of 1-m² plots. Plots were centered on the location, 10 m, 20 m, and 100 m from the location in each cardinal direction, and 14.4 m from the location in each diagonal direction (100 m distance sampled in 2008–2010 only). This grid design quantified spatial heterogeneity in the area (within 10–20 m) surrounding nests, and allowed us to test whether vegetation 0–20 m from nests differed from vegetation 100 m away. We measured vegetation height by balancing a 50 × 50 cm² cardboard plank on the canopy, and measuring the plank's height at its center. We photographed the plot with a 6.3 megapixel digital camera (Cannon EOS Digital Rebel, Canon USA, Inc., Melville, NY) mounted on an aluminum camera frame with a 1-m² base that positioned the camera for nadir images 2 m above ground level. We cropped each image to 1 m² and measured vegetation cover classes in the image using SamplePoint software (Booth et al. 2006). For each image, we classified 100 points (pixels) into categories of bare soil, green vegetation, standing dead vegetation, litter, cactus, and dung. This method produces similar results as sampling with a pin-frame (Booth et al. 2008), with the advantage that we could rapidly photograph a large number of plots, and analyze cover in the images later. We completed measurements during 27 April–13 May each year, coinciding with the peak of mountain

plover nest-site selection (Graul 1975, Knopf and Wunder 2006).

Effects of Grazing and Fire Management on Vegetation Structure

We measured vegetation in 5 grazing and fire management regimes: 1) moderate summer cattle grazing (0.6 Animal Unit Months [AUM]/ha, 3 replicate 65–130-ha pastures), 2) high intensity summer cattle grazing (1.2 AUM/ha, 2 replicate 65-ha pastures), 3) high intensity spring cattle grazing (1.2 AUM/ha, 2 replicate 130-ha pastures), 4) prescribed burns in moderately-grazed grassland (3–6 burned areas of 16–259 ha each per year), and 5) black-tailed prairie dog colonies in pastures with moderate cattle grazing (3 colonies per year). The high intensity grazing treatments were applied annually during 2004–2010. For the high intensity spring grazing treatment, cattle were provided with a ring of supplemental protein feed tubs (Vitalix, Inc., Alliance, NE) spread over approximately 1 ha in a flat, upland site, to concentrate cattle activity in their vicinity (Bailey and Welling 1999). Prescribed burn treatments included 3 areas with late-winter (Mar) burns during 2007–2009, and 3 areas with fall (Oct–Nov) burns during 2008–2010.

Each year, we sampled a randomly located grid of plots in each replicate of all 5 management regimes using a nested, systematic grid. In the intensive spring grazing treatment, the grid was located over the supplemental feed site rather than randomly. For clarity, we refer to these grids as randomly located grids and grids centered on the mountain plover nest and foraging locations as plover-occupied grids. Grids covered 100 × 60 m². We established plots (1 m²) every 20 m (24 plots). In 2007 and 2008, we added 7 nested 10 × 10 m² areas within each grid (3 additional locations per 10 × 10 m² area; 21 additional plots per grid). Thus, we sampled 45 plots per grid in 2007–2008, and 24 plots per grid in 2009–2010. We reduced sampling intensity in the latter 2 years based on 2007–2008 results. As with plover-occupied grids, randomly located grids in 2007 and 2008 quantified heterogeneity in vegetation structure at scales of 10–20 m (Gross et al. 1995). We sampled vegetation height and cover at each plot using methods described previously.

Statistical Analyses

We analyzed variation in bare soil and vegetation height among plover-occupied grids using the GLIMMIX procedure (SAS v9.3; SAS Institute, Inc., Cary, NC) in which the type of plover location (nests vs. foraging locations) and the habitat (grassland vs. prairie dog colonies vs. burns) were fixed effects and variation among years was a random effect. We tested for normality of residuals (Wilk-Shapiro statistic), and transformed response variables if necessary to meet assumptions. We analyzed variation in bare soil relative to distance from plover nests using a randomized complete block design. We compared patterns of bare soil relative to distance from nests measured during 2007–2010 (in a landscape with plovers nesting on prairie dog colonies and burns) to patterns measured in 1992 (in a landscape with moderately

grazed grassland as the primary breeding habitat; Knopf and Miller 1994).

We analyzed variation in bare soil and vegetation height among random grids in each management regime and in plover-occupied grids using analysis of variance (ANOVA) for each response variable (bare soil and vegetation height) with grid type (6 categories corresponding to 5 management regimes plus plover-occupied sites) as a fixed effect and year as a random effect.

To examine vegetation heterogeneity in random and plover-occupied grids, we calculated the variance in bare soil among the 1-m² plots in each grid. Note that this measurement of heterogeneity is not spatially explicit, as it does not account for the spatial scale at which the heterogeneity occurs. For a spatially explicit measure of heterogeneity, we examined spatial autocorrelation at separation distances of 10–15 m and 20–25 m by calculating Moran's I (Sokal and Oden 1978) using the statistical package R (www.R-project.org, accessed 29 Sep 2011).

RESULTS

Mountain Plover Nesting Habitat

Bare soil at plover locations averaged $35.1 \pm 1.6\%$ (1 SE) and vegetation height averaged 3.7 ± 0.1 cm. Percent bare soil and vegetation height at nest locations ($35.9 \pm 2.3\%$, 3.9 ± 0.1 cm, $N = 61$) and at foraging locations ($34.1 \pm 2.2\%$, 3.5 ± 0.1 cm, $N = 45$) were similar. Vegetation height did not vary among plover locations in the 3 different habitats ($F_{2,6} = 0.23$, $P = 0.805$), but bare soil at plover locations on burns was less than bare soil in prairie dog colonies and grasslands ($F_{2,6} = 7.8$, $P = 0.022$; Fig. 1). Bare soil declined at plover sites from 36.4% in May 2009 to 15.9% in May 2010 (-20.5% ; $P = 0.005$, Fig. 1) because of above-average precipitation in 2009, which was associated with a 14% increase in litter cover. Vegetation height at plover locations did not vary among years ($\chi^2 = 0.34$, $P = 0.278$).

Bare soil in 1-m² plots centered over nests sites (nest microsite) did not differ from plots 10- and 20-m distant in 2007 ($F_{2,24} = 0.26$, $P = 0.7765$; Fig. 2). Based on this finding, we increased sampling distances to 100 m during 2008–2010. For each of these years, bare soil in plots 10–100 m from the nest did not differ from bare soil at the nest microsite ($F_{3,141} = 0.04$, $P = 0.991$; Fig. 2). Bare soil at nest microsites was substantially greater during 2007–2009 (Fig. 2A) than at nest microsites measured in 1992 (Knopf and Miller 1994). In addition, bare soil declined with increasing distance from nests in 1992, but not for nests measured during 2007–2010 (Fig. 2B).

Effects of Grazing and Fire Management

Bare soil was substantially greater in random grids on prescribed burns and prairie dog colonies than in all 3 cattle grazing treatments in all 4 years (main effect of treatment: $F_{5,15} = 15.00$, $P < 0.001$; year \times treatment interaction: $\chi^2 = 0.85$, $P = 0.18$; Fig. 3A). Bare soil surrounding plover-occupied sites was similar to random grids on burns and prairie dog colonies in all years (Fig. 3A). Although mean bare soil in the intensive grazing treatments increased

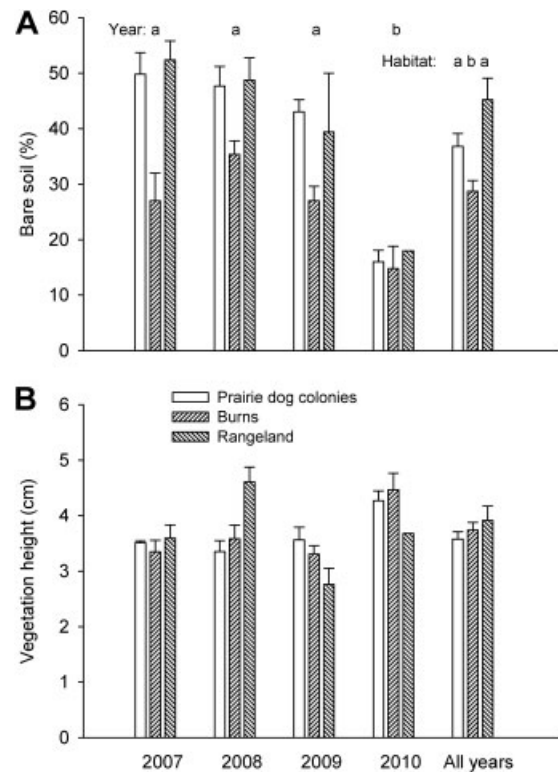


Figure 1. Percent bare soil (A) and vegetation height (B) surrounding mountain plover nest and foraging locations in 3 different habitats in north-eastern Colorado, 2007–2010. Bars with different letters indicate significant differences ($P < 0.05$) among years and habitat for bare soil (no significant year \times habitat interaction; $P = 0.43$). We did not detect significant differences for vegetation height.

between 2007 and 2008 as we had expected (both relatively dry growing seasons), mean bare soil declined substantially under intensive grazing following 2 wet growing seasons, such that mean bare soil was very similar in all 3 grazing treatments in 2009 and 2010 (Fig. 3A).

Effects of management regimes on vegetation height varied among years (year \times treatment interaction: $\chi^2 = 2.29$, $P = 0.065$), because patterns following growing seasons with below-average precipitation (measurements in spring of 2007 and 2008) differed from patterns following above-average precipitation (spring of 2010; Fig. 3B). In 2007 and 2008, vegetation height was consistently below 4 cm on burns and prairie dog colonies, and at plover-occupied sites. Vegetation height was similar in both intensive grazing treatments (4.4–5.7 cm), and significantly taller under moderate grazing (>7 cm; Fig. 3B). Following above-average precipitation in 2009, vegetation height in 2010 was similar across all 3 grazing treatments (>9.5 cm), was intermediate for prairie dog colonies (5.8 cm), and was lowest for burns (4.4 cm) and grids at plover-occupied sites (4.4 cm; Fig. 3B). Patterns for both bare soil and vegetation height in the 5 different management regimes suggest random locations on prairie dog colonies were most similar to plover-occupied sites following dry growing seasons (2007 and 2008), whereas random locations on burns were most similar to plover-occupied sites following a wet growing season (2010; Fig. 3A,B).

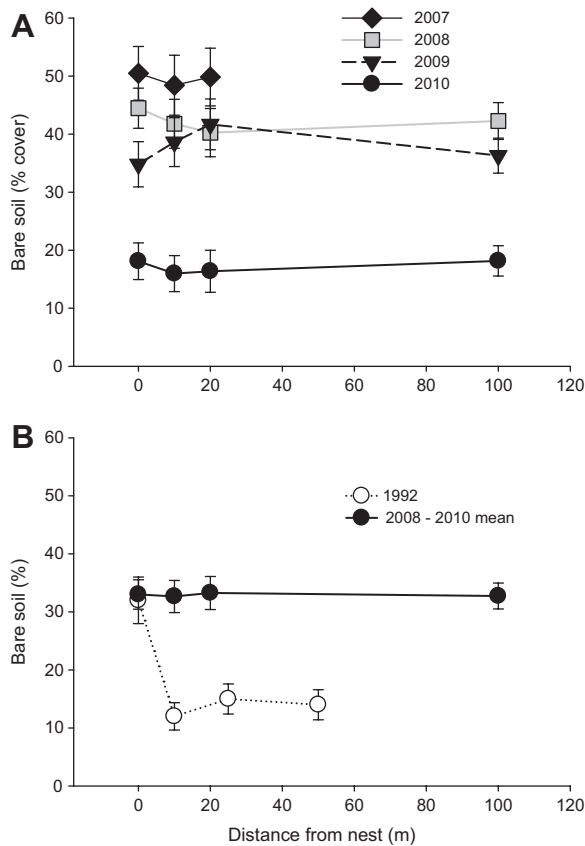


Figure 2. Comparison of (A) variation in bare soil with increasing distance from the nest for each of the 4 years sampled in this study, and (B) variation in bare soil with increasing distance from the nest for nests sampled in a landscape with burns and prairie dog colonies (mean of 2007–2010) versus a landscape lacking burns and prairie dog colonies (1992; Knopf and Miller 1994).

In all grid types and distance classes, Moran's *I* was consistently near zero (mean = -0.07 for plover-occupied sites and mean = 0.04 for random grids) indicating that bare soil was randomly distributed in all management regimes and in plover-occupied sites (Table 1). Variance in bare soil was significantly greater in random grids on prairie dog colonies compared to random grids on all 3 grazing treatments (treatment: $P = 0.0009$, year: $P = 0.06$, year \times treatment: $P = 0.65$, Table 1). Variance in bare soil at plover-occupied sites was greater than the

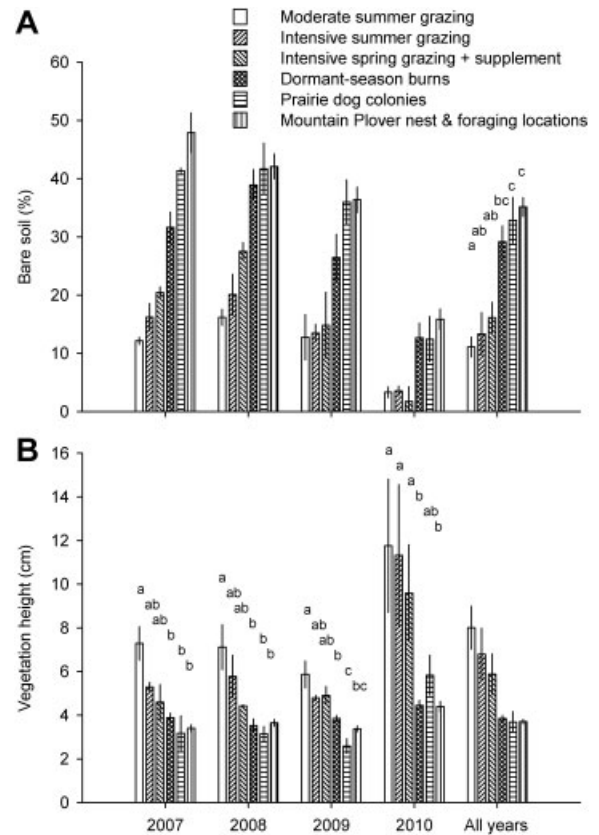


Figure 3. Comparison of bare soil and vegetation height measured in randomly located grids in each of 5 management regimes versus grids surrounding mountain plover nest and foraging locations in northeastern Colorado, 2007–2010. Bars with different letters differ significantly at the $P < 0.05$ level. For bare soil, treatment differences were consistent across all 4 years (year \times treatment interaction, $P = 0.18$); for vegetation height, treatment differences showed evidence of variation among years (year \times treatment interaction, $P = 0.065$), so differences are indicated for each year separately.

variance in the 3 grazing treatments and less than the variance on prairie dog colonies, but differences were not statistically significant. Overall, plover-occupied sites were characterized by a fine-scale mosaic of prostrate vegetated patches interspersed with high amounts of bare soil in a given square meter, with this fine-scale pattern distributed over a broad (>100 -m radius) area. In addition, plover-occupied sites were not characterized by a patchy distribution of bare soil at scales of 10–20 m (Moran's *I*, Table 1).

Table 1. Comparison of mean bare soil and within-site spatial variation in bare soil for plover-occupied sites and random sites in 5 different management regimes in shortgrass steppe of northeastern Colorado in 2007 and 2008. Patterns did not differ between 2007 and 2008, so values shown are means for both years combined. Moran's *I* measures local spatial autocorrelation in bare soil for plots separated by the distance classes indicated, where values near zero indicate a lack of spatial autocorrelation, and values approaching 1 or -1 indicate strong positive or negative spatial autocorrelation. Variance measures variability among plots in bare soil regardless of their proximity to one another. Values with different superscripted letters within a column differ at the $P < 0.05$ level.

	Mean bare soil (%)	Mean Moran's <i>I</i>		Mean within-grid variance
		10–15 m	20–25 m	
Moderate summer grazing	14.2 ^{ab}	0.01	-0.07	49.4 ^a
Intensive summer grazing	18.1 ^{ab}	0.09	-0.10	117.3 ^a
Intensive spring grazing + supplement	24.0 ^{abc}	0.01	0.05	172.4 ^a
Prescribed burn	36.5 ^{bc}	0.04	-0.01	177.0 ^{ab}
Active prairie dog colony	41.5 ^c	0.11	0.05	394.7 ^b
Mountain plover locations	44.3 ^c	-0.03	-0.11	240.8 ^{ab}

DISCUSSION

Where rangelands are predominantly managed for livestock production, there is often an economic incentive to use livestock grazing, rather than other historical disturbances, to manage for ecosystem services such as wildlife habitat. However, we found that intense cattle grazing did not generate mountain plover nesting habitat. Rather, habitat conditions selected by plovers were more effectively created through prescribed burning or prairie dog grazing. Our findings indicate that recognition and restoration of the role of historical disturbances other than large herbivore grazing can be important for sustaining native grassland wildlife species.

Our findings also illustrate the challenge of identifying habitats important to declining wildlife species when such habitats have been eliminated from the landscape (McCleery et al. 2007). Past studies in a landscape lacking fire and prairie dogs indicated that mountain plovers nested in moderately grazed grassland at microsites with a greater percentage of bare soil, but did not select sites with more bare soil over a larger surrounding area (Fig. 2B; Gaul 1975, Knopf and Miller 1994). Following the restoration of fire and an order-of-magnitude expansion in prairie dog colony area, mountain plovers now nest in areas with bare soil and prostrate vegetation distributed over a substantially larger (>100-m radius) area. This shift may have resulted from an absence of disturbances necessary to expose more bare soil over large areas in previous decades. Mountain plovers are cryptically colored, resembling bare soil when viewed from above, and often sit motionless in the presence of avian predators. Both crypsis and early detection of approaching predators may explain their selection of large areas with a fine-scale mosaic of bare soil and prostrate vegetation, consistent with observations for upland-nesting shorebirds in other grasslands (Koivula and Rönka 1998, Whittingham et al. 2002).

The strong response of nesting mountain plovers to burns and prairie dog colonies suggests a coevolutionary relationship, and hence that fire and prairie dog grazing may have been important historical disturbances in the ecosystem. Although we did not measure reproductive success in our study, selection for historical disturbances is likely related to increased plover reproduction and/or survival. Adult survivorship of mountain plovers breeding on black-tailed prairie dog colonies in Montana increased in drought years and decreased in wet years (Dinsmore 2008). We found large patches with >35% bare soil occurred on burns and prairie dog colonies in dry years (2007–2008), whereas bare soil declined in all habitats following above-average precipitation. In shortgrass steppe, mountain plovers nesting on prairie dog colonies had 3-fold greater brood rearing success compared to mountain plovers nesting on grassland without prairie dogs (Dreitz 2009). In Montana, mountain plover populations can persist on large prairie dog colony complexes (Dinsmore et al. 2005). Collectively, these studies are consistent with our finding that prairie dog colonies provide large patches with a greater percentage of bare

soil exposure, whereas such conditions are rare in moderately grazed grassland without prairie dogs.

Little is known about breeding success of mountain plovers in burned landscapes, although Svingen and Giesen (1999) found 49% nesting success on a burn in shortgrass steppe, which was similar to nesting success in other breeding habitats (Dinsmore et al. 2010). Even so, additional studies of nesting and brood-rearing success are needed to evaluate the value of burns as breeding habitat. We also note that plover-selected sites were structurally more similar to random prairie dog grids after dry years (when prairie dogs could exert greater control over plant growth), but were more similar to random burn grids following a wet year (when plant growth could outpace prairie dog consumption, and fuel loads for burns were high). This finding suggests burns may be a particularly effective management tool in semiarid grasslands following years with average or above-average precipitation.

Shortgrass steppe is one of the most resistant grasslands worldwide to large herbivore grazing, in terms of plant productivity, cover, and species composition (Milchunas and Lauenroth 1993, Milchunas et al. 2008). We found that even intense cattle grazing could not generate as much bare soil as found on burns and prairie dog colonies. These findings can be explained by adaptations of the dominant warm-season grasses (*Bouteloua gracilis* and *Buchloe dactyloides*) to aridity and intensive herbivory, including a prostrate canopy, minimal stem investment, substantial biomass allocation belowground or to stolons, and rapid growth following defoliation and small precipitation pulses (Milchunas and Lauenroth 1989, Milchunas et al. 2008). Cattle can only graze shortgrasses to ≥ 1 cm above crown height (e.g., Varnamkhasti et al. 1995), creating a refugia to support regrowth. In contrast, prairie dogs defoliate plants more frequently, closer to crown level, and year-round, all of which contribute to the loss of shortgrass dominance and increased bare soil on colonies. Indeed, on prairie dog colonies, *B. gracilis* populations are genetically different from populations grazed only by large herbivores in terms of their physiological responses to defoliation (Jaramillo and Detling 1988). Differences in herbivore body size, foraging patterns, digestive system, and plant responses to defoliation patterns all may contribute to our finding of non-substitutable effects of a large ungulate herbivore versus a small rodent herbivore on vegetation structure and bird habitat.

MANAGEMENT IMPLICATIONS

The use of prescribed burning and management to maintain or increase areas occupied by black-tailed prairie dogs both appear to be effective and complementary means to manage for mountain plover breeding habitat in shortgrass steppe. Fire use is controversial in semiarid grasslands due to perceived loss of reserve forage for livestock and lack of shrub encroachment. However, depending on their timing (following average or above-average precipitation) and spatial configuration (<50% of a pasture), burns can be used to manage wildlife habitat without negatively affecting

forage availability to cattle (Augustine and Milchunas 2009, Augustine et al. 2010). Managers must also consider the cost of implementing burns. Programs to transfer fire management knowledge and capacity from mesic to semiarid grasslands could assist in reducing such costs. Although we found that fires and black-tailed prairie dogs had similar effects on mountain plover habitat, prairie dog conservation may be a particularly effective means to sustain mountain plover habitat in the western Great Plains because effects on vegetation structure are more stable in space and time than are the effects of fires. The development of economic incentives or markets to compensate for livestock production losses associated with prairie dogs may be one means to advance mountain plover habitat conservation on privately-owned grasslands. These conservation-production tradeoffs also necessitate that land managers clearly define desired outcomes for management to provide multiple ecosystem goods and services.

ACKNOWLEDGMENTS

Funding for this study was provided by the United States Department of Agriculture, Agricultural Research Service (USDA-ARS). We thank P. McCusker for assistance with all aspects of data collection throughout the study. We thank Drs. Daniel Milchunas and Susan Skagen for helpful reviews of the manuscript, and the many technicians and students that assisted in the field or with photo analyses, including E. Hardy, D. Smith, J. Ling, T. Odell, J. Baker, S. Podolak, E. Klarquist, R. Moore, M. Ashby, J. Thomas, T. Smith, P. Freeman, M. Mortenson, and A. Whitman. We thank N. Clark, R. Reichert, B. Humphrey, and K. Philbrook for facilitating our work on Pawnee National Grassland.

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Associate Editor: Daniel Twedt.

APPENDIX A. SUMMARY OF SITES SURVEYED EACH YEAR.

Summary of the number of sites and points visited during an initial survey conducted each year to identify areas with mountain plovers within the study area in northeastern Colorado. Black-tailed prairie dog colonies included in the surveys were 16–245 ha during 2007–2009, and 5–126 ha in 2010. Burns were 16–259 ha. Random and non-random grassland sites (all with no recent history of prairie dogs or burns) were 259 ha each. Intensively grazed rangeland sites were 65–130 ha. The surveys employed point counts during 2008–2010, but not in 2007 (see Methods Section).

	Black-tailed prairie dog colonies		Recent burns		Random grassland sites		Non-random grassland sites		Intensively grazed grassland sites	
	Colonies	Points	Burns	Points	Pastures	Points	Pastures	Points	Pastures	Points
2007	9		3				3		4	
2008	9	53	10	76	12	120	3	29	4	32
2009	18	83	7	46	12	119	3	28	4	32
2010	41	107	6	21			3	30	4	32
Total	77	243	26	143	24	239	12	87	16	96